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THE SYSTEMATIC POSITION OF *RHYNIELLA PRAECURSOR* HIRST & MAULIK (COLLEMBOLA). THE EARLIEST KNOWN HEXAPOD

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The remains of Rhyniella praecursor were first described by Hirst and Maulik (1926) from the Rhynie Chert in Scotland. They consisted of four heads and were assigned to the order Insecta. Tillyard (1928) pointed out that R.praecursor was a collembolon which belonged to the Poduridae (now Poduromorpha) because it had simple antennae consisting of four nearly equal segments and typical mouth parts. Further head capsules, a thorax with 3 pairs of legs, and antennae were discovered by W. Cran and all fragments were described and figured by Scourfield (1940a,b) who came to the conclusion that Rhyniella belonged to the Arthropleona probably the Entomobryomorpha because of the reduction of thorax I. Massoud (1967) reexamined the specimens publishing some new figures and reinterpreting the drawings of Scourfield. He concluded that thorax I was present and well developed and that the maxillae were styliform. Later, after regrinding revealed a further specimen which included the posterior abdomen showing a furca, Whalley & Jarzembowski (1981) published a photograph of this new specimen finally confirming its identification as a collembolon.

Our recent examination of the specimens has revealed some morphological features not previously described and these, together with a study of the characters observed earlier, strongly suggest that Rhyniella belongs to the Isotomidae.

Geological Age of Strata

Rhynie chert was considered to be of Devonian age when Rhyniella was first discovered (Hirst & Maulik 1926). Criticism has been levelled at this dating of the collembolan fossil by Crowson (1985) because of the finding of a thysanopteran nymph in the deposit which was clearly a later contaminant. However it has been shown that the Collembola are securely embedded in the rock and that there was only a single phase of mineralisation (Whalley & Jarembowski 1981). Most recent dating using argon/argon techniques have confirmed the chert as being over 400 million years old.

Habitat description

The habitat in which the Rhyniella probably lived has been described as a swamp, small lake, pond or marsh (Tasch 1957). Evidence from the plants, which are mainly vascular cryptograms, points to a fast penetration of a silicate rich solution resulting in rapid preservation of the cells. Leptocarid crustacea, mites and other arachnids have also been found in the deposit and are much more common than the Collembola.

Summary of description of Rhyniella praecursor Hirst & Maulik 1926

A detailed redescription of the specimens will be published elsewhere but a summary of the characters, mainly new, is given below: ocelli 8+8;

antennal segments nearly equal in length; postantennal organ small, oval, slightly lateral to antennal base; no apical bulb on ant.IV, pin seta probably present; mandible with toothed head and molar plate and maxilla, stipes, cardo, fulcrum, hypopharynx and usual associated structures present; labium with setae set in tubercles; fronto-clypeal sclerite very well developed; frontal margin of head with many short curved setae; outer maxillary lobe present; head anteriorly triangular, rectangular posterior to base of mouth parts; long thin claw; abd.III & IV approximately equal in length; abd.V & VI equal and about half abd.IV in length: manubrium rather longer than dens; dens cylindrical; mucro short broad with two large teeth; cuticle pigmented and with primary tubercles only; plurichaetose as shown by many small setal insertions.

Earlier Family Determinations

The families to which Rhyniella has been assigned since its discovery and the reasons given are listed in table I.

Table I. Family classifications of Rhyniella praecursor.

Taxon	Author	Reason
Poduromorpha	Tillyard (1928)	proportions of antennae mouth parts
Entomobryomorpha possibly Protentomobryidae	Scourfield (1940)	elongate body, lack of thorax I, equal body segments, molar plate
Rhyniellidae	Paclt (1956)	no reason given
Protentomobryidae	Salmon (1964)	no reason given
Neanuridae	Massoud (1967)	thorax I present, maxillae styliform
Isotomidae	Greenslade, this work	thorax I absent, mandibular molar plate, simple oval PAO, elongate body, segments nearly equal, head shape, 8+8 ocelli.

Discussion of characters used for earlier family determinations

1. Lengths of segments of appendages. The nearly equal segments of the antennae was considered by Tillyard (1928) to be an indication that Rhyniella belonged to the Poduromorpha. However some genera in the Isotomidae also have nearly equal segments to these appendages. For instance, antennal segment proportions are listed in brackets below for the following genera: Isotomodes (10:15:15:23), Folsomides (3:4:4:7) Ballistura (6:8:8:11), Archisotoma (11:20:20:25). Rhyniella appears to have ant.III equal to or slightly longer than ant.IV. This character is found in some littoral genera: Hydroisotoma (1:1); Axelsonia (12:11) both Isotomidae, Pseudanurida (1:1), Neanuridae and Coenoletes (15:14), Coenaletidae. The character in a more extreme form is diagnostic of the Dicyrtomidae and most Tomoceridae.

2. Thoracic segmentation. Scourfield (1940a,b) interpreted specimens

as lacking thorax I but with well developed thorax II and III (Fig.1). This led him to suggest that Rhyniella had affinities with the Entomobryidae (now the Entomobryoidea). Massoud (1967) believed from the position of insertion of legs that the first segment seen on the specimens was thorax I. (Fig.2). Although the specimen examined by Scourfield and Massoud is now lost, it is clear from another specimen in lateral view (No.38230 BMNH) that leg I is inserted immediately behind the head and not ventrally on the first segment visible. The first two segments of Rhyniella are about equal in length and plurichaetose. This supports the interpretation that th.I is absent in Rhyniella since in all known Collembola where it is present, it is much smaller than th.II & III and has a single row setae at most.

3. Mouth parts. Massoud interpreted the mandible as lacking a molar plate while Scourfield observed and drew one. On specimens 38225 & 38226 (BMNH) a complete set of mouthparts is visible: mandible with molar plate and maxillae with basal structures (Figs 3-6)

4. Postantennal organ. A structure illustrated by Scourfield designated "round projection" (specimen 1, 27765) was also illustrated by Massoud (1967 Fig.A) but without comment. It is in the position normally occuppied by the postantennal organ in Collembola and we consider it to be homologous with that organ.

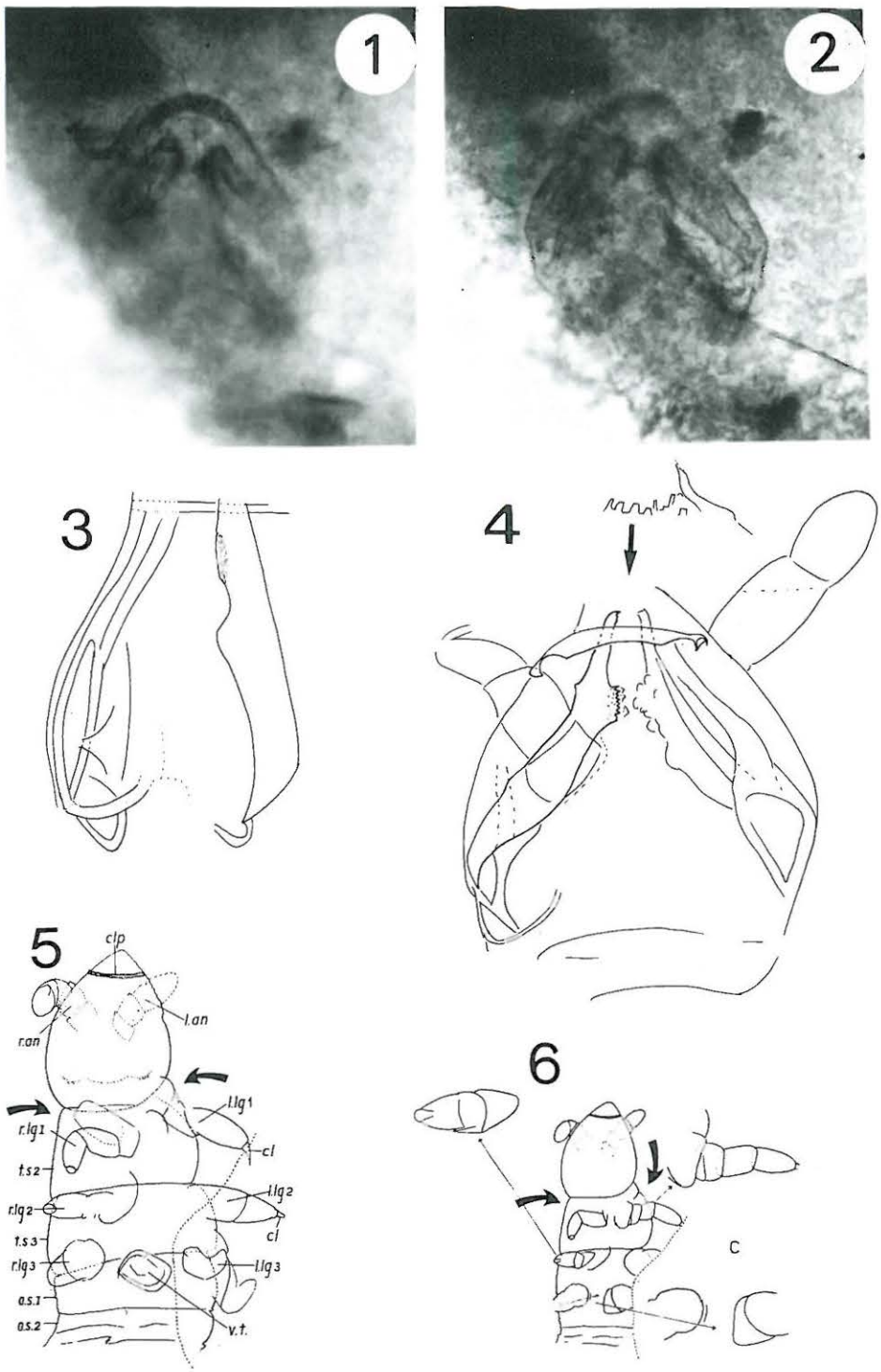
5. Shape of head. The shape of a Rhyniella head is triangular anteriorly and rectangular posteriorly and not simply triangular as asserted by Hirst and Maulik. The base of the mouthparts which is the widest point, being about the mid point. Only in the Entomobryiodea is this seen in extant Collembola; this group possesses an extra two rows of setae posterior to the ocelli, pp and cv (Deharveng 1977), compared to the Poduroidea.

Family affinity

Of the three suborders of Collembola, Rhyniella clearly cannot belong to the Symphypleona or Neelipleona because of its elongate body and separate abdominal segments. The third, the Arthropleona is divided into two superfamilies of which the Poduroidea are exluded on the absence of thorax I. This leaves the Entomobryoidea in which there are currently 11 families. The Entomobryidae, Cyphoderidae, Paronellidae, Tomoceridae, Oncopoduridae, Actaletidae, Coenaletidae and Microfalculidae are excluded by a combination of the following characters; possession of 8+8 ocelli, a postantennal organ, near equal body segments, unsubsegmented antennae, short appendages and short mucro. The remaining three families are the two monobasic fossil families Rhyniellidae and Protentomobryidae, and the Isotomidae. All characters to date which have been found, suggest the placement of Rhyniella praecursor in the Isotomidae and, from the description, Protentomobrya walkeri Folsom, the type species of the Protentomobryidae, may also correctly belong in the same family, the characters of which are given below.

Diagnosis of Isotomidae

Antennal segments separate, not subsegmented, thorax I non setose, pronotum either absent or small; mandible with molar plate and maxilla present; postantennal organ nearly always present; head triangular anteriorly, posteriorly rows of pp and cv setae present; abdominal segments approximately equal, neither III or IV markedly longer than any other, scales and flexed macrosetae absent; claw with single inner margin.



Figs 1-6 Rhyniella praecursor: Fig.1,2, Photographs of the mouthparts of specimen 38225, Fig 3,4, drawings of mouthparts of same specimen, Fig 5, specimen 38228 as drawn by Scourfield (1940), Fig 6, same specimen drawn by Massoud (1967).

Diagnosis of Rhyniella Hirst & Maulik 1926

Plurichaetose; cuticle, pigmented and with primary granules only; 8 + 8 ocelli; simple, small, oval PAO present; fronto-clypeal sclerite very well developed; abdomen IV, V and VI separate; furca present and attached to abdomen IV ventrally; manubrium parallel sided; dens cylindrical, about half as long as manubrium; mucro with two teeth at least; habitus of Archisotoma.

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Abbreviations: BMNH, British Museum (Natural History, London); abd., abdomen; th., thorax, ant., antenna.